Windthrows increase soil carbon stocks in a central Amazon forest

Leandro T. dos Santos1,*, Daniel Magnabosco Marra1,2,3,*, Susan Trumbore2, Plínio B. de Camargo1, Robinson I. Negrón-Juárez3, Adriano J. N. Lima1, Gabriel H. P. M. Ribeiro1, Joaquim dos Santos1, and Niro Higuchi1

1Laboratório de Manejo Florestal, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil
2Biogeochemical Processes Department, Max Planck Institute for Biogeochemistry, Jena, Germany
3AG Spezielle Botanik und Funktionelle Biodiversität, Universität Leipzig, Leipzig, Germany
4Centro de Energia Nuclear na Agricultura, Piracicaba, Brazil
5Climate Sciences Department, Lawrence Berkeley National Laboratory, Berkeley, USA
*These authors contributed equally to this work.

Correspondence to: Daniel Magnabosco Marra (dmarra@bgc-jena.mpg.de)

Received: 15 September 2015 – Published in Biogeosciences Discuss.: 7 December 2015
Revised: 10 February 2016 – Accepted: 16 February 2016 – Published: 2 March 2016

Abstract. Windthrows change forest structure and species composition in central Amazon forests. However, the effects of widespread tree mortality associated with wind disturbances on soil properties have not yet been described in this vast region. We investigated short-term effects (7 years after disturbance) of widespread tree mortality caused by a squall line event from mid-January of 2005 on soil carbon stocks and concentrations in a central Amazon terra firme forest. The soil carbon stock (averaged over a 0–30 cm depth profile) in disturbed plots (61.4 ± 8.2 Mg ha⁻¹, mean ±95% confidence interval) was marginally higher (p = 0.09) than that from undisturbed plots (47.7 ± 13.6 Mg ha⁻¹). The soil organic carbon concentration in disturbed plots (2.0 ± 0.17%) was significantly higher (p < 0.001) than that from undisturbed plots (1.36 ± 0.24%). Moreover, soil carbon stocks were positively correlated with soil clay content (r² = 0.332, r = 0.575 and p = 0.019) and with tree mortality intensity (r² = 0.257, r = 0.506 and p = 0.045). Our results indicate that large inputs of plant litter associated with large windthrow events cause a short-term increase in soil carbon content, and the degree of increase is related to soil clay content and tree mortality intensity. The higher carbon content and potentially higher nutrient availability in soils from areas recovering from windthrows may favor forest regrowth and increase vegetation resilience.

1 Introduction

Tropical forests contain about 44% (383 Pg C) of the approximately 860 Pg C stored in forests worldwide, with soils accounting for 32% of the total carbon stocks (Quéré et al., 2009; Lal, 2004). Global emissions due to changes in land use and soil cultivation are estimated to be 136 Pg C since the industrial revolution (Lal, 2004; Houghton, 1999). However, there are few estimates of emissions by the decomposition and mineralization of organic carbon in soils following natural disturbances (Lal, 2004), presumably because we assume there is a balance between rapid losses that follow disturbance and recovery between disturbances at the larger spatial scales.

The effects of large-scale natural disturbances (i.e., wind disturbances) on carbon stocks and cycling due to the increase of litter inputs promoted by widespread tree mortality, the fraction of this carbon that persists in soil organic matter, and how long it is stabilized are poorly known in both in tropical and temperate forests (Foster et al., 1998; Turner et al., 1998). In temperate forests, newly exposed soil due to wind disturbance can cover from ca. 10% (Peterson et al., 1990) up to 60% of the surface (Beatty, 1980; Putz, 1983). In a three-species temperate forest in Slovakia, no organic carbon was lost at two windthrow sites within 3.5 years after disturbance, but shifts occurred within organic layers and mineral soil toward decomposed organic matter (Don et al., 2012). In Amazonian forests, where windthrows are a ma-
Wind disturbances are frequent in the western and central Amazon, (Nelson et al., 1994; Espírito Santo et al., 2010; Negrón-Juárez et al., 2010). In this large region, windthrows are associated with torrential rains and very strong winds (16 m s$^{-1}$) known as downbursts (Nelson et al., 1994; Garstang et al., 1998). The widespread tree mortality creates canopy gaps with a wide range of sizes (from few square meters up to thousands of hectares; Nelson et al., 1994; Negrón-Juárez et al., 2010, 2011) and affects forests at the landscape level (Marra et al., 2014). It has been reported that these large gaps have a potential effect on carbon cycling (Chambers et al., 2013) and can promote tree species diversity by allowing a diverse cohort of species with a broad range of life history strategies (Chambers et al., 2009; Marra et al., 2014) and allometry (Ribeiro et al., 2014).

In the tropics, winds break and uproot trees causing strong soil disturbances (e.g., increasing leaves and wood debris and changing morphology and nutrient availability; Schaetzl et al., 1989; Lugo, 2008). Treefall gaps can also change microclimate conditions such as light intensity and create a variety of microsites, which can be separated into canopy, trunk, and root/uprooted sites (Putz, 1983). These microsites have important features that drive soil and vegetation recovery after disturbance (Putz, 1983; Schaetzl et al., 1989; Vitousek and Denslow, 1986). They can differ in microbial activity (Batjes, 1996) and enhance the colonization of fast-growing species that help in the assimilation of nutrients and soil carbon, which in turn can contribute to quickly restore the forest canopy through succession (Putz, 1983). This rapid recycling of nutrients potentially enhances the resilience of tropical forests to natural disturbances (Schaetzl et al., 1989; Ostertag et al., 2003; Lugo, 2008). However, how complex and hyperdiverse tropical forests such as the Amazon will respond in a scenario of higher frequency of extreme weather events (Coumou and Rahmstorf, 2012; Cai et al., 2014) is still not clear.

We assessed the effects of wind disturbances on soils of a large terra firme forest in central Amazon. We hypothesized that windthrows forming large canopy gaps ($\geq$2000 m$^2$) affect the soil carbon content via litter and wood debris deposition and decomposition, and that the soil carbon content is controlled by the interaction of tree mortality intensity, clay content, and depth. To test our hypothesis we addressed the following questions:

1. Are there differences in soil carbon stocks between disturbed and undisturbed areas, and how do possible variations compare to other tropical and temperate forests worldwide?
2. What is the importance of soil texture (clay content) on soil organic carbon content in wind disturbed areas?
3. Does tree mortality intensity influence soil carbon stocks?

2 Methods

2.1 Study site

This study was conducted in a large terra firme forest, ca. 100 km from Manaus, Amazonas, Brazil (Fig. 1). We sampled soils from the Estação Experimental de Silvicultura Tropical (EEST) of the Instituto Nacional de Pesquisas da Amazônia (INPA) and from a contiguous forest, adjacent to
the Ramal-ZF2 road. The forest adjacent to the Ramal-ZF2 road is owned and administered by the Superintendência da Zona Franca de Manaus (SUFRAMA). Mean annual temperature in this region was 26.7 °C (1910–1983; Chambers et al., 2004), and rainfall ca. 50 km east of our study site averaged to 2610 mm yr⁻¹ (1980–2000; Silva et al., 2003). From July to September there is a distinct dry season with usually less than 100 mm of rain per month. The forest at the studied region has a closed canopy, high tree species diversity, and a dense understory (Braga, 1979).

The soils of the Amazon region are old and complex, with type and texture influenced by local topographical variations. At the studied region, the relief is undulating with altitude ranging from 40 to 180 m a.s.l. Soils on upland plateaus and the upper portions of slopes have high clay content (Oxisols), while soils on slope bottoms and valleys have high sand content (Spodosols; Telles et al., 2003) and are subject to sporadic inundations (Junk et al., 2011). The yellow Oxisols are found primarily on plateaus and slopes. In general, the soils are well drained and have low fertility, low pH, low cation exchange capacity, high aluminum concentration, and low organic carbon (Ferraz et al., 1998; Telles et al., 2003).

### 2.2 Tree mortality estimates

In January of 2005, a single squall line event propagating across the Amazon caused widespread tree mortality over large areas (Negrón-Juárez et al., 2010), including ca. 250 ha of terra firme forest in the study area (Fig. 1). Tree mortality directly caused by this event was quantified at landscape level through the correlation of plot-based measurements and changes on the fractions of green vegetation (GV) and non-photosynthetic vegetation (NPV) calculated from Landsat images – see Negrón-Juárez et al. (2010) for a detailed method description. This metric, validated by Negrón-Juárez et al. (2011), allowed us to sample soils across an extent tree mortality gradient 0–70 %, including from small- to large-sized gaps and patches of old-growth forest not affected by the 2005 windthrows (Marra et al., 2014).

### 2.3 Soil sampling

We sampled soils during the dry season (July–September) of 2012 (7 years after disturbance) according to the degree of disturbance intensity measured as tree mortality (%). In total, 16 plots with dimensions of 25 m × 10 m were selected along three pairs of transects, with 200 (E1), 600 (E2), and 1000 m (E3) length (Fig. 1). The transects cross several toposequences and include local variations of soils and forest structure among plateaus, slopes, and valleys. In this study, we only considered plots established on plateaus, which were more severely affected by the 2005 windthrows (Marra et al., 2014). Although our samples covered soils types from Oxisols to Spodosols, we reduced strong soil attribute variations related to topography by excluding slope and valley areas.

In each of our 16 selected plots, we sampled six soil profiles 5 m from each other. We took samples from three depths (0–10, 10–20, and 20–30 cm) using an auger. For soil bulk density, samples were also collected in the three depths in one or two profiles per plot using 5 cm tall cylinders with a volume of 98 cm³. Altogether we collected 288 soil samples for carbon analysis (16 plots × 6 depth profiles × 3 depths) and 63 samples for density (21 depth profiles × 3 depths; Fig. 1).

### 2.4 Soil analysis

Before performing soil analyses, we removed leaves, twigs, and roots from our samples. Samples were then sieved, dried, and homogenized by grinding (< 2 mm). The soil carbon con-

---

**Table 1.** Average concentrations of soil organic carbon content (SOC), soil carbon stocks (SCSs), bulk density (BD), and clay, silt, and sand average concentrations in transect 1 (E1), transect 2 (E2), and transect 3 (E3). Values in brackets represent the standard error of the mean.

<table>
<thead>
<tr>
<th>Transect</th>
<th>Depth profile (cm)</th>
<th>SOC (%)</th>
<th>SCS (Mg ha⁻¹)</th>
<th>SOC (%)</th>
<th>SCS (Mg ha⁻¹)</th>
<th>BD (g cm⁻³)</th>
<th>Clay (%)</th>
<th>Silt (%)</th>
<th>Sand (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>E1</td>
<td>0–10</td>
<td>3.72 (0.28)</td>
<td>31.00 (5.07)</td>
<td>2.48 (0.24)</td>
<td>20.18 (0.75)</td>
<td>0.74 (0.07)</td>
<td>69.42</td>
<td>21.97</td>
<td>8.56</td>
</tr>
<tr>
<td></td>
<td>10–20</td>
<td>2.31 (0.13)</td>
<td>22.82 (1.97)</td>
<td>2.05 (0.22)</td>
<td>19.24 (0.74)</td>
<td>0.97 (0.09)</td>
<td>69.04</td>
<td>22.42</td>
<td>8.54</td>
</tr>
<tr>
<td></td>
<td>20–30</td>
<td>1.79 (0.13)</td>
<td>16.61 (1.76)</td>
<td>1.71 (0.17)</td>
<td>13.06 (0.44)</td>
<td>0.98 (0.10)</td>
<td>68.69</td>
<td>22.78</td>
<td>8.53</td>
</tr>
<tr>
<td>E2</td>
<td>0–10</td>
<td>3.27 (0.19)</td>
<td>25.50 (1.42)</td>
<td>–</td>
<td>–</td>
<td>0.89 (0.09)</td>
<td>57.41</td>
<td>19.31</td>
<td>22.25</td>
</tr>
<tr>
<td></td>
<td>10–20</td>
<td>1.79 (0.09)</td>
<td>19.87 (0.84)</td>
<td>–</td>
<td>–</td>
<td>1.15 (0.11)</td>
<td>67.59</td>
<td>22.42</td>
<td>8.54</td>
</tr>
<tr>
<td></td>
<td>20–30</td>
<td>1.36 (0.07)</td>
<td>15.11 (1.59)</td>
<td>–</td>
<td>–</td>
<td>1.31 (0.10)</td>
<td>60.23</td>
<td>19.41</td>
<td>19.34</td>
</tr>
<tr>
<td>Average</td>
<td>0–10</td>
<td>2.11 (0.14)</td>
<td>21.52 (1.80)</td>
<td>1.17 (0.14)</td>
<td>11.36 (3.44)</td>
<td>1.24 (0.10)</td>
<td>22.63</td>
<td>10.33</td>
<td>67.04</td>
</tr>
<tr>
<td></td>
<td>10–20</td>
<td>1.31 (0.08)</td>
<td>17.48 (3.08)</td>
<td>0.82 (0.09)</td>
<td>10.69 (2.63)</td>
<td>1.36 (0.06)</td>
<td>57.82</td>
<td>19.11</td>
<td>23.08</td>
</tr>
<tr>
<td></td>
<td>20–30</td>
<td>1.13 (0.10)</td>
<td>16.50 (2.90)</td>
<td>0.75 (0.07)</td>
<td>10.14 (2.63)</td>
<td>1.41 (0.09)</td>
<td>24.78</td>
<td>10.94</td>
<td>63.32</td>
</tr>
<tr>
<td></td>
<td>Average</td>
<td>2.89 (0.13)</td>
<td>25.90 (2.06)</td>
<td>1.58 (0.19)</td>
<td>14.90 (3.18)</td>
<td>0.95 (0.09)</td>
<td>50.55</td>
<td>17.30</td>
<td>32.15</td>
</tr>
<tr>
<td></td>
<td>10–20</td>
<td>1.71 (0.07)</td>
<td>20.05 (1.34)</td>
<td>1.13 (0.13)</td>
<td>14.11 (2.76)</td>
<td>1.16 (0.10)</td>
<td>50.45</td>
<td>17.90</td>
<td>31.65</td>
</tr>
<tr>
<td></td>
<td>20–30</td>
<td>1.37 (0.06)</td>
<td>16.01 (1.27)</td>
<td>0.98 (0.10)</td>
<td>11.31 (1.91)</td>
<td>1.19 (0.10)</td>
<td>51.95</td>
<td>17.51</td>
<td>30.54</td>
</tr>
</tbody>
</table>
Before performing statistical tests, we tested our data set for normality and homoscedasticity. To address our first question we use factorial ANOVA and compared undisturbed/low-disturbance plots (tree mortality < 5 %, hereafter referred as undisturbed forest) with those that experienced higher disturbance intensities (tree mortality ≥ 5 %, hereafter referred as disturbed forest). In total we sampled 5 plots in undisturbed forest and 11 plots in disturbed forest. In the disturbed forest plots were set in disturbed patches varying from 900 m² to ca. 17 ha in area (Marra et al., 2014). To address our second question, we compared the SCS values from our study with those from different tropical and temperate forests. We performed all analysis in R 3.0.1 platform (R Core Team, 2014) and produced Figs. 2–5 using the ggplot2 package (Wickham, 2009). We produced the Fig. 1 using the ArcMap GIS extension of the ArcGIS 10 software (ESRI, 2011).

### 3 Results

Soils from the disturbed forest had higher mean values of SCS and SOC than those from the undisturbed forest. This was true for all three depths we sampled (Table 1). SCS values averaged over 0–30 cm were 61.4 ± 8.2 Mg ha\(^{-1}\) (mean ± 95 % confidence interval) for disturbed and 47.7 ± 13.6 Mg ha\(^{-1}\) for undisturbed forest (\(p = 0.09\) and \(F = 3.191\); Fig. 2a). For the same depth profile, SOC values were 2.0 ± 0.17 % for the disturbed and 1.36 ± 0.24 % for the undisturbed forest (\(F = 16.74\) and \(p < 0.001\); Fig. 2b).

The soil clay content in the entire study area ranged from 2.0 to 71.5 % averaged over 0–30 cm depth. This large variation in soil texture led to a large variation in the concentration of soil organic carbon (SOC) and soil carbon stocks (SCSs). The SOC in the upper samples (0–10 cm) had values ranging from 0.29 to 6.62 % and mean of 2.57 ± 0.13 %. For the same depth interval, values of SCS ranged from 3.79 to 60.55 Mg ha\(^{-1}\) with a mean value of 23.34 ± 2.01 Mg ha\(^{-1}\). Overall, bulk density increased with depth, while SOC and SCS decreased (Table 1). We found no difference comparing soil clay content between the disturbed and the undisturbed forest (\(F = 2.648\) and \(p = 0.108\)). The fact that there was no difference between the two types of forest confirms...
Table 2. Estimates of soil carbon stock (SCS) from this and other studies conducted in different tropical, subtropical, and temperate forests.

<table>
<thead>
<tr>
<th>Author</th>
<th>Region</th>
<th>Forest type</th>
<th>Successional stage/management</th>
<th>SCS (Mg ha⁻¹) (0–10 cm)</th>
<th>Soil type/description</th>
</tr>
</thead>
<tbody>
<tr>
<td>dos Santos et al. (2016)</td>
<td>Manaus, AM, Brazil</td>
<td>Amazon terra firme forest (closed canopy)</td>
<td>Undisturbed/old-growth forest</td>
<td>14.9 ± 4.7</td>
<td>Oxisols/Spodosols</td>
</tr>
<tr>
<td>Telles et al. (2003)</td>
<td>Manaus, AM, Brazil</td>
<td>Amazon terra firme forest (closed canopy)</td>
<td>Disturbed (windthrow) forest</td>
<td>25.9 ± 6.4</td>
<td>Oxisols/Spodosols</td>
</tr>
<tr>
<td>Floresta Nacional do Tapajós, PA, Brazil</td>
<td>Amazon terra firme forest (closed canopy)</td>
<td>Old-growth forest</td>
<td>19.2 ± 4.7</td>
<td>Oxisols</td>
<td></td>
</tr>
<tr>
<td>Trumbore et al. (1995)</td>
<td>Paragominas, PA, Brazil</td>
<td>Amazon terra firme forest (closed canopy)</td>
<td>Old-growth forest</td>
<td>12.5 ± 2.8</td>
<td>Spodosols</td>
</tr>
<tr>
<td>Camargo et al. (1999)</td>
<td>Paragominas, PA, Brazil</td>
<td>Amazon terra firme forest (closed canopy)</td>
<td>Old-growth forest</td>
<td>26 ± 2.8</td>
<td>Oxisols</td>
</tr>
<tr>
<td>Neil et al. (1996)</td>
<td>Aripuanã, RO, Brazil</td>
<td>Amazon terra firme forest (open canopy)</td>
<td>Old-growth forest</td>
<td>32.3 ± 4.6</td>
<td>Oxisols</td>
</tr>
<tr>
<td>Neil et al. (1997)</td>
<td>Aripuanã, RO, Brazil</td>
<td>Amazon terra firme forest (open canopy)</td>
<td>Secondary forest</td>
<td>27.4 ± 3.6</td>
<td>Oxisols</td>
</tr>
<tr>
<td>Osto Prêto do Oeste, RO, Brazil</td>
<td>Amazon terra firme forest (open canopy)</td>
<td>Old-growth forest</td>
<td>29.7 ± 3.6</td>
<td>Oxisols</td>
<td></td>
</tr>
<tr>
<td>Porto Velho, RO, Brazil</td>
<td>Amazon terra firme forest (open canopy)</td>
<td>Old-growth forest</td>
<td>48.1 ± 3.6</td>
<td>Oxisols</td>
<td></td>
</tr>
<tr>
<td>Cacauçu, RO, Brazil</td>
<td>Amazon terra firme forest (open canopy)</td>
<td>Old-growth forest</td>
<td>62 ± 2.8</td>
<td>Oxisols</td>
<td></td>
</tr>
<tr>
<td>Víthema, RO, Brazil</td>
<td>Amazon terra firme forest (open canopy)</td>
<td>Old-growth forest</td>
<td>39.3 ± 3.6</td>
<td>Oxisols</td>
<td></td>
</tr>
<tr>
<td>Freigl et al. (1995)</td>
<td>Aripuanã, RO, Brazil</td>
<td>Amazon terra firme forest (open canopy)</td>
<td>Old-growth forest</td>
<td>50.6 ± 3.6</td>
<td>Oxisols</td>
</tr>
<tr>
<td>Mai et al. (2009)</td>
<td>Conquista D’Oeste, MT, Brazil</td>
<td>Amazon terra firme forest (open canopy)</td>
<td>Old-growth forest</td>
<td>65.3 ± 3.6</td>
<td>Oxisols</td>
</tr>
<tr>
<td>Trumbore et al. (1995)</td>
<td>Paragominas, PA, Brazil</td>
<td>Amazon terra firme forest (closed canopy)</td>
<td>Old-growth forest</td>
<td>39.3 ± 3.6</td>
<td>Oxisols</td>
</tr>
<tr>
<td>Telles et al. (2003)</td>
<td>Nova Monte Verde, MT, Brazil</td>
<td>Amazon terra firme forest (open canopy)</td>
<td>Old-growth forest</td>
<td>35.4 ± 3.6</td>
<td>Oxisols</td>
</tr>
<tr>
<td>Pimenteiras do Oeste, RO, Brazil</td>
<td>Amazon terra firme forest (open canopy)</td>
<td>Old-growth forest</td>
<td>46.5 ± 3.6</td>
<td>Oxisols</td>
<td></td>
</tr>
<tr>
<td>São José do Xingu, MT, Brazil</td>
<td>Seasonal semi-deciduous forest</td>
<td>Old-growth forest</td>
<td>33.4 ± 3.6</td>
<td>Oxisols</td>
<td></td>
</tr>
<tr>
<td>Santa Luzia D’Oeste, RO, Brazil</td>
<td>Amazon terra firme forest (open canopy)</td>
<td>Old-growth forest</td>
<td>36.1 ± 3.6</td>
<td>Oxisols</td>
<td></td>
</tr>
<tr>
<td>Thobimba, RO, Brazil</td>
<td>Amazon terra firme forest (open canopy)</td>
<td>Old-growth forest</td>
<td>46.8 ± 3.6</td>
<td>Oxisols</td>
<td></td>
</tr>
<tr>
<td>Mai et al. (2010)</td>
<td>Poções c Lacerda, MT, Brazil</td>
<td>Amazon terra firme forest (closed canopy)</td>
<td>Old-growth forest</td>
<td>47.6 ± 3.6</td>
<td>Oxisols</td>
</tr>
<tr>
<td>Ribeiro et al. (2000)</td>
<td>Ecuador</td>
<td>Amazon terra firme forest (open canopy)</td>
<td>Old-growth forest</td>
<td>95.6 ± 3.6</td>
<td>Andic Humitropepts</td>
</tr>
<tr>
<td>Batjes (2001)</td>
<td>Senegal</td>
<td>Equatorial forest</td>
<td>Old-growth forest</td>
<td>23 ± 3.6</td>
<td>Ortho Ferralsol³</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Old-growth forest</td>
<td>35 ± 3.6</td>
<td>Planthic Ferralsol³</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Old-growth forest</td>
<td>30 ± 3.6</td>
<td>Eutric Regosol³</td>
</tr>
<tr>
<td>Powers and Schlesinger (2002)</td>
<td>Costa Rica</td>
<td>Tropical wet forest</td>
<td>Old-growth forest</td>
<td>82.2 ± 3.6</td>
<td>Teopodudal³, Dystropept³ and Dystrandept³</td>
</tr>
<tr>
<td>Veldkamp et al. (2003)</td>
<td>Costa Rica</td>
<td>Tropical moist forest</td>
<td>Old-growth forest</td>
<td>64 ± 3.6</td>
<td>Oxisols</td>
</tr>
<tr>
<td>Marin-Striplat et al. (2009)</td>
<td>Puerto Rico</td>
<td>Subtropical wet forest life zone</td>
<td>Old-growth forest</td>
<td>96 ± 3.6</td>
<td>Oxisols</td>
</tr>
<tr>
<td>Grimm et al. (2008)</td>
<td>Barro Colorado Island</td>
<td>Semi-deciduous moist tropical forest</td>
<td>Old-growth forest</td>
<td>31 ± 3.6</td>
<td>Oxisols, Cambisols</td>
</tr>
<tr>
<td>Neumann-coel et al. (2011)</td>
<td>Panama</td>
<td>Tropical moist forest</td>
<td>Old-growth forest (100-year-old)</td>
<td>69.4 ± 3.6</td>
<td>Homogenous, silty clay and clay, pH values from 4.4 to 5.9</td>
</tr>
<tr>
<td>Ngo et al. (2013)</td>
<td>Singapore</td>
<td>Coastal hill dipterocarp forest</td>
<td>Old-growth forest</td>
<td>22.1 ± 3.6</td>
<td>Very acidic and infertile</td>
</tr>
<tr>
<td>Don et al. (2012)</td>
<td>Slovenia</td>
<td>Mixed temperate forest</td>
<td>Old-growth forest</td>
<td>47 ± 3.6</td>
<td>Dystric Cambisols</td>
</tr>
<tr>
<td>Kramer et al. (2004)</td>
<td>Tongass National Forest, Alaska, USA</td>
<td>Coastal temperate rain forest</td>
<td>Old-growth forest (128-year-old)</td>
<td>47 ± 3.6</td>
<td>Heterogeneous (Spodosols, Histosols and Inceptisols)</td>
</tr>
<tr>
<td>Huntingdon and Ryan (1990)</td>
<td>Hubbard Brook Experimental Forest, New Hampshire, USA</td>
<td>Northern hardwood forest</td>
<td>Secondary forest (218-year-old)</td>
<td>32 ± 3.6</td>
<td>Acidic Type, Lithic and Aquic Haplorthods</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Secondary forest (65-year-old)</td>
<td>34 ± 3.6</td>
<td></td>
</tr>
</tbody>
</table>

* IBGE, 2004; ¹ USA Soil Taxonomy; ² FAO, 1998; World Reference Base for Soil Resources (WRB); ³ Oa horizon.

our hypothesis that the tree mortality is the major vector of the changes we observed.

Along the entire sampled area (disturbed and undisturbed forest), the SCS was positively correlated with soil clay content (Fig. 3a) and with tree mortality intensity (Fig. 3b). When constraining the tree mortality gradient into three disturbance categories defined as tree mortality intensity (%), we found no differences in SCS (F = 1.67 and p = 0.226; Fig. 4a). However, SCS was 61.1 ± 12 Mg ha⁻¹ in the disturbance category 3 (tree mortality ≥ 50 %) vs. 43.1 ± 17.2 Mg ha⁻¹ in disturbance category 1 (tree mortality < 5 %). The SOC in the disturbance category 2 (5 % ≤ tree mortality <50 %) was marginally higher than that from category 1 (Tukey HSD, p = 0.066; Fig. 4b).

4 Discussion

4.1 Estimates of soil carbon stocks

As expected, our results were between those values found in the two soils types (Oxisols and Spodosols) evaluated in a previous study also conducted at the EEST (Telles et al., 2003), in which SCS values for 0–10 cm were reported as 14.9 ± 3.18 Mg ha⁻¹ (Table 2). However, the overall SCS value (23.3 ± 2.01 Mg ha⁻¹) and that from our disturbed forest (25.9 ± 2.06 Mg ha⁻¹) were greater than those reported by Telles et al. (2003). Such differences indicate an increasing in SOC and SCS 7 years following disturbance.

The soils from our study area also had different SCS values from those reported for other regions of the Brazilian Amazon (i.e., same/similar soil types; Table 2). For the 0–10 cm profile, when comparing to old-growth forests in the Pará state, the mean SCSs of our undisturbed and disturbed forests were lower and similar, respectively (Trumbore et al.,...
that reported for the 0–30 cm depth profile from an equatorial forest in Senegal, Africa (Batjes, 2001). For the 0–10 cm depth profile, our disturbed forest had SCS values higher than that reported for an old-growth coastal hill dipterocarp forest in Singapore (Ngo et al., 2013) and a 68-year-old secondary coastal temperate rain forest in southeast Alaska (Kramer et al., 2004), both in different soil types. In contrast, our disturbed forest had lower SCS values than those reported for other temperate forests in Europe (Don et al., 2012) and North America (Huntington and Ryan 1990; Kramer et al., 2004). This was true for both non-harvested and harvested forests, in which nutrient exportation via logging has an opposite effect than that of wind disturbances (nutrient inputs).

4.2 Changes in carbon stocks and clay concentration in the soil

Soil clay content was positively correlated with the SOC (Pearson’s $r = 0.907$) at 0–30 cm depth profile and consequently with SCS (Pearson’s $r = 0.575$). This relationship between SOC and clay content was shown in other studies (Powers and Schlesinger, 2002; Kahle et al., 2002). The soil organic matter can form aggregates stabilizing the clay surface and the age of the soil carbon at the same depth increases with clay content (Telles et al., 2003). However, the clay content is not always a good predictor of SOC (Torn et al., 1997; Powers and Schlesinger, 2002; Telles et al., 2003). Thus, the method we applied in this study would be better applied in studies involving the same soil type and origin. In other situations, the mineralogical composition (i.e., including the type of clays) may be a better predictor of SOC than just the percentage of clay itself.

Due to the proximity of our plots, we assume climatic and geological aspects to be constant. Thus, the importance of soil texture on carbon stocks in our study site reflects a local pattern. Here we focused on assessing the effects of the existing Amazon tree mortality gradient (Espírito Santo et al., 2010; Chambers et al., 2013) on SOC and SCS, which is why we excluded valleys and selected plots along transects crossing forest patches with different disturbance inten-
soil attributes at the landscape level. In this region, the observed organic carbon enrichment derived from widespread tree mortality might also be related to the fast establishment and growth of pioneer species in heavily disturbed areas (Chambers et al., 2009; Marra et al., 2014).

In contrast, according to Lin et al. (2003), the Fushan Experimental Forest, which has experienced frequent windstorms, did not regain any nutrients following disturbance. This, in turn, has limited local tree growth (shown as lower canopy height) and, consequently, decreased carbon input into the soil. Thus, more intense mortality regime can also be expected to change forest dynamics, and eventually decrease SCS and nutrient cycling. The effects might depend on forest stature, successional stage (i.e., floristic composition and forest structure attributes such as tree density, basal area, and biomass), and tree mortality intensity, often controlled by the speed and duration of wind gusts (Lugo et al., 1983; Garstang et al., 1998). In our study area, fast vegetation regeneration could even reduce short-term losses of carbon associated with the 2005 windthrows, which had an estimated emission (assuming the carbon from all felled trees emitted to the atmosphere at once) of ca. 0.076 PgC, equivalent to 50 % of the deforestation during that same year (Higuchi et al., 2011; Negrón-Juárez et al., 2010).

The size of gaps in which we observed significant increase on soil carbon content (gaps from 0.1 up to 17 ha) indicates that windthrows – apart from influencing tree species composition, forest structure, and forest dynamics (Chambers et al., 2013; Marra et al., 2014) – also change soil attributes. The nutrients released in this process might have an important feedback on vegetation resilience and recovery following disturbance. To determine how much of the added soil carbon is stabilized in a long term, future studies should assess soil carbon stocks and soil organic carbon along a chronosequence including wind-disturbed terra firme forests with different time since disturbance. Since wind is a major disturbance agent in western and central Amazon, more precise estimates of soil carbon stocks need to consider and reflect differences in tree mortality regimes at the landscape level.

Acknowledgements. We gratefully acknowledge the workers from the EEST/INPA for giving support with the fieldwork, and the lab team of the CENA-USP and the Laboratório Temático de Solos e Plantas (LTSP/INPA) for giving support with the soil analyses. We also acknowledge the SUFRAMA for allowing us to access part of the study area. At last, we acknowledge Edzo Velkamp, an anonymous referee, and Hermann F. Jungkunst for providing valuable comments during the revision of this article. This study was financed by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) within the project SAWI (Chamada Universal MCTI/N14/2012, Proc. 473357/2012-7) and the INCT – Madeiras Tecnológico (CNPq) within the project SAWI (Chamada Universal MCTI/N14/2012, Proc. 473357/2012-7).
de Manejo Florestal (LMF/INPA). Robinson I. Negron-Juarez was supported by the Office of Science, Office of Biological and Environmental Research of the US Department of Energy under contract no. DE-AC02-05CH11231 as part of Next-Generation Ecosystems Experiments (NGEE Tropics) and the Regional and Global Climate Modeling (RGCM) Program.

The article processing charges for this open-access publication were covered by the Max Planck Society.

Edited by: E. Veldkamp

References


Putz, F. E.: Treefall pits and mounds, buried seeds, and the importance of soil disturbance to pioneer trees on Barro Colorado Island, Panama, Ecol., 64, 1069–1074, 1983.


R Core Team: R: A language and environment for statistical computing, available at: http://www.r-project.org (last access: 1 October 2015), 2014.

